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Research article

Modelling interactive effects of multiple disturbances on a coastal lake ecosystem: Implications for management

Hannah F.E. Jones*, Deniz Özkundakci [1], Chris G. McBride, Conrad A. Pilditch, Mathew G. Allan, David P. Hamilton [2]

Environmental Research Institute, University of Waikato, Private Bag 3105, Hamilton, New Zealand

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ABSTRACT

Coastal lakes, also known as temporarily open/closed estuaries or intermittently closed and open lakes and lagoons, are common worldwide, are typically sites of high biodiversity and often contain abundant macrophyte populations. Anthropogenic stressors such as increased nutrient and sediment loading have adverse effects on submerged macrophytes, and when closed, the lack of tidal flushing makes coastal lakes highly susceptible to eutrophication. Lake openings to the sea may occur naturally, but many coastal lakes are also opened artificially, often to reduce inundation of surrounding land. Here we used a coupled hydrodynamic-ecological model (DYRESM-CAEDYM), modified to include dynamic feedback between submerged macrophyte biomass and sediment resuspension, to explore the interactive effects of multiple disturbances (openings, eutrophication and climate change) on the dynamics of primary producers in a coastal lake (Waituna Lagoon) in South Island, New Zealand. Our results indicate that with exposure to high external nutrient loads, the frequent disturbances caused by artificial openings prevent sustained dominance by algae (algal biomass averaged 192 g C m^{-2} with artificial openings compared to 453 g C m^{-2} with no openings). However, under current nutrient loading, climate change is likely to enhance the effects of eutrophication on the system (algal biomass averaged 227 g C m^{-2} with climate change compared with 192 g C m^{-2} for current climate). The model provides a decision-support tool to guide lake management in setting limits for nutrient loads and managing the opening regime, in order to prevent eutrophication and the potential collapse of the macrophyte community.

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1. Introduction

Coastal lakes are common worldwide, and are often highly valued for ecological, recreational and cultural reasons (Haines et al., 2006; Hume et al., 2007; Ticehurst et al., 2007). Also known as temporarily open/closed estuaries (TOCEs) or intermittently closed and open lakes and lagoons (ICOLLs), these ecosystems contain abundant and diverse submerged macrophyte communities that can sustain high levels of biodiversity (Schallenberg et al., 2010). In many estuaries and coastal lakes, however, anthropogenic influences such as catchment land use conversions to pasture have increased sediment and nutrient loads, resulting in declining macrophyte populations (e.g., Burkholder et al., 2007; Drake et al., 2010). Because coastal lakes are generally shallow, the lack of tidal flushing during periods of closure causes them to be highly susceptible to increases in contaminant loads, often leading to eutrophication (e.g., Drake et al., 2010; Haines et al., 2006). In some cases, the complete loss of submerged macrophytes followed by increases in dominance of phytoplankton has occurred (*sensu* Scheffer et al., 1993; Walker and McComb, 1992). Furthermore, the wide-range in physico-chemical conditions relating to opening/closing may subject submerged macrophyte populations in coastal lakes to additional stressors; in particular, widely fluctuating salinity and highly variable water levels that cause desiccation (Riddin and Adams, 2012; Robertson and Funnell, 2012).

Management approaches for coastal lakes often encompass artificial opening to the sea when water levels are high, to reduce

* Corresponding author. Present address: Waikato Regional Council, Private Bag 3038, Hamilton, New Zealand.
E-mail address: jones.hfe@gmail.com (H.F.E. Jones).
[1] Present address: Waikato Regional Council, Private Bag 3038, Hamilton, New Zealand.
[2] Present address: Australian Rivers Institute, Griffith University, 170 Kessels Rd, Brisbane, Australia.

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inundation of surrounding land (which is often used for agricultural purposes) or to flush nutrients from the lake (e.g. Schallenberg et al., 2010). This practice may be detrimental to ecosystem function however as openings can change entrance morphology, hydrodynamics, and cause desiccation of fringing wetlands (Haines et al., 2006). By contrast, artificial openings may reduce the effects of eutrophication, although the extent of water quality improvement is likely dependent on the degree of tidal flushing, which is generally not readily controlled (Schallenberg et al., 2010).

Regime shifts between macrophyte and phytoplankton dominated states have been observed in many coastal lakes, with unidirectional changes (i.e., permanent loss of submerged macrophytes) in some systems (e.g., Gerbeaux, 1993; Viaroli et al., 2008), and apparent multiple shifts in others (e.g., Mitchell, 1989; Riddin and Adams, 2012). In a number of coastal or shallow lake systems worldwide, long-term disturbances associated with catchment development (into agricultural land use, causing increased nutrient and sediment loading), water level fluctuations, manipulations of fish populations, and even the use of tributyltin (TBT), have been associated with such regime shifts (Blindow et al., 1993; Sayer et al., 2006; Schallenberg and Sorrell, 2009; Viaroli et al., 2008). For example, the East Kleinemonde and St Lucia estuaries in South Africa, both coastal lakes, exhibit shifts between macrophyte and macroalgae, or phytoplankton dominated states, dependent on opening status and salinity (Riddin and Adams, 2010; Taylor et al., 2006). In the South Island of New Zealand, submerged macrophytes in Te Waihora (Lake Ellesmere) were completely lost in 1968 following a severe storm that was preceded by long-term land use change in the catchment. The lake has been highly turbid and phytoplankton-dominated ever since (Gerbeaux, 1993). In contrast, Tomahawk Lagoon (also located in the South Island, New Zealand) has shifted between submerged macrophyte and phytoplankton dominance on an irregular cycle, with each phase lasting between 1 and 5 years (Mitchell, 1989). Similarly, Waituna Lagoon on the south coast of the Southland of New Zealand, which is the focus of the current study, has experienced cycles of submerged macrophyte and phytoplankton dominance due to recent variations in nutrient load from the catchment (Schallenberg et al., 2017). However, to what extent nutrient loads would have to be managed to maintain submerged macrophytes in these lakes before a complete collapse occurs is still poorly understood.

Warming temperatures and altered meteorological conditions caused by climate change may exert additional stress to these systems. Recent research indicates that the growth of cyanobacteria and filamentous algae will be enhanced by a warmer climate in shallow lake ecosystems (e.g., Trochine et al., 2011; Elliott, 2012; Paerl and Paul, 2012; Rolighed et al., 2016). These findings have important implications for the management of a range of aquatic ecosystems because proliferation of benthic and planktonic filamentous algae may influence transitions between alternate states (e.g. Genkai-Kato et al., 2012; Stevenson, 2014). In New Zealand, climate change may increase the potential for regime shifts in shallow or coastal lakes by enhancing the effects of eutrophication (e.g. increasing frequency of cyanobacterial blooms due to warmer water temperature), altering catchment-derived nutrient and sediment loading, and increasing wind-induced resuspension of bottom sediments which ultimately increases water column turbidity (Hamilton et al., 2012). Moreover, altered hydrology and warmer temperatures are likely to alter water levels in coastal lakes, disturbances already linked to regime shifts (Blindow et al., 1993; Scheffer and van Nes, 2007; Randsalu-Wendrup et al., 2016).

In this study, we used a deterministic model to explore drivers of ecological dynamics (i.e., the relationship between primary producers and their environment) in Waituna Lagoon, a coastal lake in South Island, New Zealand. Dynamic process-based ecological models are frequently used to provide guidance for sustainable management of aquatic ecosystems, particularly with regard to setting limits for nutrient loads and water levels (e.g., Marcé et al., 2010; Machado and Imberger, 2012; Parparov and Gal, 2012; Trolle et al., 2014). Moreover, these models can provide a useful tool for exploring ecological interactions across a broad suite of pressure gradients over long (decadal) time scales. Such complex models are rarely used to investigate the interactive effects of multiple disturbances on ecological dynamics in shallow aquatic ecosystems (Kuiper et al., 2014) and we are not aware of any application in this context on coastal lakes. Waituna Lagoon is especially well suited as a study site as it historically had large submerged macrophyte beds (Schallenberg et al., 2017), but has recently been subject to substantially increased nutrient loads following land-cover changes (McDowell et al., 2016). Observations of declining macrophyte populations and increased algal abundance have led to concern that the lagoon is at risk of shifting to a phytoplankton-dominated state (e.g., Robertson and Funnell, 2012).

For the purpose of this study, the model was primarily designed to further our understanding of the influence of, and interactions amongst, frequent disturbance (artificial lake openings) and chronic disturbance (increases in anthropogenic nutrient loading and climate change) on the potential for shifts in dominance of primary producers in coastal lakes. By utilizing a dynamic process-based ecological model, the insights gained in this study are likely to be applicable to similar systems. The application of the model to Waituna Lagoon may also be used as a decision-support tool to provide guidance on potential management options for the lagoon (involving managing nutrient loads and opening regimes) to prevent the further decline and collapse of the macrophyte population. Specifically, we asked the following questions: (i) what nutrient load reductions may be necessary to prevent long-term dominance of phytoplankton and prevent total collapse of submerged macrophytes in the system, and (ii) what are the potential interactive effects on ecosystem dynamics (with special emphasis on the biomass of primary producers) of artificial lake openings, climate change and nutrient loading? To answer these questions, we modified the coupled hydrodynamic-ecological model (DYRESM-CAEDYM; e.g., Gal et al., 2009) to include dynamic feedback between submerged macrophyte biomass and sediment resuspension. We then simulated a broad range of scenarios developed in consultation with other scientists, stakeholders, managers and iwi (indigenous Māori) with cultural connections to the lagoon, to explore the effects of multiple disturbances on the ecosystem. Given the value and occurrence of these ecosystems globally, the model framework presented here will be useful to inform management of such systems elsewhere.

2. Materials and methods

2.1. Study site

Waituna Lagoon (46° 34′ S, 168° 36′ E) is a small, shallow coastal lake in South Island, New Zealand (Fig. 1). Coastal lakes of this type have low to moderate freshwater surface inflows, are separated from the sea by a gravel barrier, and naturally remain closed for periods of many months to years (Kirk and Lauder, 2000). Although the barrier at Waituna Lagoon allows for some seepage between the lagoon and the sea, it is opened artificially usually once per year by the local environmental management agency (Environment Southland) to reduce inundation of surrounding farmland. When open, the mean depth in the lagoon is less than 1 m and the surface area is c. 8 km^2, but when closed the mean depth can increase to 1.6 m and the surface area to 16 km^2. Salinity in the lagoon ranges from <1 to 34 psu, depending on open/closed state, and opening

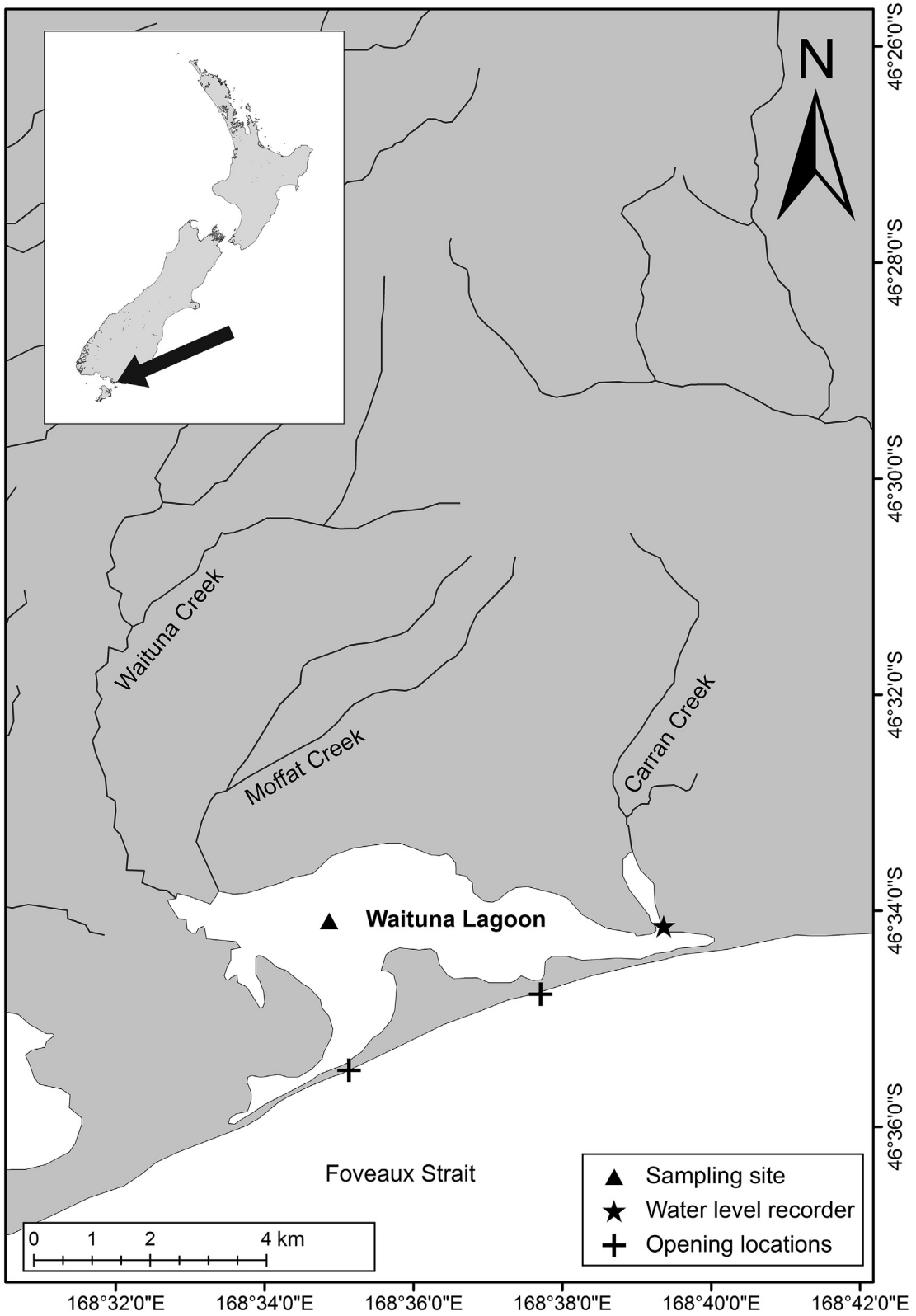

Fig. 1. Waituna Lagoon, South Island, New Zealand, showing locations of the monitoring site (for monthly samples of temperature, salinity, dissolved oxygen, nutrient and chlorophyll *a* concentrations), water level recorder and opening locations.

events markedly reduce nutrient and chlorophyll *a* concentrations due to the high degree of tidal flushing provided by the lagoon morphology (Schallenberg et al., 2010, 2017).

Waituna Lagoon is part of the Awarua wetland complex, a Ramsar site with high diversity of endemic and threatened species. The aquatic plant community in the lagoon is characterised by extensive beds of *Ruppia polycarpa* and *R. megacarpa*, with other species such as *Myriophyllum triphyllum* and *Lamprothamnium macropogon* sometimes locally abundant (e.g., Johnson and Partridge, 1998; Sutherland and Taumoepeau, 2011). *R. megacarpa* is recognised as a key species in Waituna Lagoon (Robertson and Funnell, 2012). Recent surveys have indicated increased presence of nuisance epiphytic macroalgae (such as *Ulva intestinalis*, *Cladophora* sp., and *Spirogyra* sp.) loosely attached to submerged macrophytes, which may affect *Ruppia* growth (e.g. Robertson and Stevens, 2009; Stevens and Robertson, 2010).

The Waituna Lagoon catchment currently consists of a mixture of peatland managed by the Department of Conservation (7%), indigenous and exotic forest (6%), sheep and beef farming (26%) and dairy farming (57%). Land use in the catchment has changed rapidly in recent years, mostly due to conversion of sheep and beef to dairy farming, and increasing trophic status in the lagoon has been linked to this land use intensification (McDowell et al., 2016).

2.2. Model description

The one-dimensional (1D) hydrodynamic model DYRESM (Dynamic Reservoir Simulation Model; V3.1) was coupled with the aquatic ecological model CAEDYM (Computational Aquatic Ecosystem Dynamics Model V3.3), to simulate temperature, salinity, dissolved oxygen and nutrient concentrations, and primary producer dynamics in Waituna Lagoon. The use of a 1D model was driven by the need for long-term (i.e., decadal) simulations to resolve the effect of disturbances on components of the lagoon ecosystem (e.g. submerged macrophyte populations) that respond over time scales of years. Three-dimensional (3D) ecological modelling may be appropriate for resolving horizontal circulation, but requires significantly more resources in terms of data for parameterisation, calibration, and computing time, effectively precluding long-term simulations in this study as was shown in other similar situations (e.g. Mooij et al., 2010).

DYRESM-CAEDYM was developed by the Centre for Water Research, University of Western Australia. DYRESM resolves the vertical distribution of temperature, salinity, and density, and the vertical mixing processes in lakes and reservoirs. CAEDYM simulates time-varying fluxes that regulate biogeochemical variables (e.g. nutrient species, phytoplankton biomass), with comprehensive process representations for carbon, nitrogen, phosphorus, and dissolved oxygen cycles, and inorganic suspended solids. Many applications of DYRESM-CAEDYM have been made to different lakes worldwide, including in New Zealand (e.g. Burger et al., 2008; Gal et al., 2009; Özkundakci et al., 2011; Trolle et al., 2011), and detailed descriptions of the model equations can be found in Robson and Hamilton (2004) and Romero et al. (2004).

The biogeochemical variables in CAEDYM may be configured according to the goals of the model application and availability of data. Based on phytoplankton sampling carried out by Environment Southland from April to October 2011, which indicated dominance by small unicellular non-heterocystous cyanophytes, cryptophytes and diatoms, these three phytoplankton groups were simulated in CAEDYM. The interactions between phytoplankton growth and losses, sediment mineralisation, and decomposition of particulate organic matter influence phosphorus and nitrogen cycling in the model, and are described in detail in Appendix A (Fig. A1). Fluxes of dissolved inorganic and organic nutrients from the bottom sediments are dependent on temperature and dissolved oxygen concentration of the water layer immediately above the sediment surface (e.g., see Burger et al., 2008).

CAEDYM also has provision for simulation of one submerged macrophyte group and up to four macroalgae groups. Data for parameterisation and calibration/validation were not considered adequate to have confidence in simulating the dynamics of individual macrophyte or macroalgae species. One group of submerged macrophytes (conceptualised as *Ruppia*) and one group of macroalgae were thus simulated. We developed the macrophyte module in CAEDYM specifically for species such as *Ruppia*, and implemented feedback between macrophyte biomass and bottom shear stress, as macrophytes are known to influence resuspension of inorganic and organic sediments (e.g., Hamilton and Mitchell, 1996; see Appendix A for further details). The default macrophyte algorithm in CAEDYM relates macrophyte productivity to changes in light, temperature and salinity (Hipsey et al., 2011). For this study, the salinity limitation function was altered so that respiration could be increased at salinities above an optimum, as high salinities may be detrimental to *R. polycarpa* germination and growth (Gerbeaux, 1989; Sim et al., 2006). A self-shading function (see Appendix A; Fig. A1c) was added to the macrophyte growth algorithm in order to regulate peak biomass of *Ruppia* during ideal growth conditions (Haese and Pronk, 2011). Further details on *Ruppia*-specific algorithms and the feedback between macrophyte biomass and bed shear stress implemented in this study are given in Appendix A. As the *Ruppia* beds are mostly located above sea level, desiccation of the beds when the lagoon is opened is also likely to significantly affect *Ruppia* populations (Johnson and Partridge, 1998). Thus, the model was configured to represent the lagoon as a series of vertical layers of between 0.1 and 0.5 m depth. Desiccation of *Ruppia* was represented by the reduction of *Ruppia* biomass to a minimum value when the water level decreased to expose *Ruppia* within the upper-most model layer.

2.3. Model input

DYRESM-CAEDYM was run at hourly time steps between October 2001 and October 2011, with daily averaged input data and daily output data at midday. A one-year "warm up" period, for which the first year of input data was looped, was implemented to address uncertainty in the model initialisation. Meteorological data required for the simulation period were obtained from the National Climate Database (CliFlo: NIWA's National Climate Database on the Web; URL: http://cliflo.niwa.co.nz/; Retrieved 16/01/2012) for the Tiwai Point climate station (46° 35′ S, 168° 23′ E) located c. 15 km west of Waituna Lagoon. Data included daily average values of air temperature (°C), shortwave radiation (W m^{-2}), estimated cloud cover (fraction of whole sky), vapour pressure (hPa), wind speed (m s^{-1}) and daily sums of rainfall (m d^{-1}).

Prior to model setup, a water balance was used to describe the flow of water in and out of the lagoon, in order to estimate outflow for which no data was available. Evaporation from the lagoon was calculated as a function of wind speed and air vapour pressure from the daily average evaporative heat flux (Imerito, 2007). Daily values for stream inflow discharges were obtained from a continuous flow recorder for the largest inflow (Waituna Creek; see Fig. 1) and discharge for other surface water inputs (other named and unnamed streams) was based on concurrent gauging (see Appendix A; Table A1). Groundwater inputs directly into the lagoon were estimated based on an annual catchment water balance and groundwater seepage estimates (Rissman et al., 2012). Outflow (i.e., barrier seepage when the lagoon was closed and outflow through the opening when open) was subsequently estimated as a residual term of an otherwise complete water balance for the simulation

period. Tidal inflows and outflows were included as input in the model for periods when the lagoon was open. Tidal flows were derived from the lagoon tidal prism and tide heights for Bluff (46° 36′ S, 168° 21′ E, c. 20 km west of Waituna Lagoon) obtained from the NIWA (National Institute of Water and Atmosphere) tide forecaster (NIWA tide forecaster; URL: http://www.niwa.co.nz/services/online-services/tide-forecaster; Retrieved 16/01/2017). Daily values for tidal input data were derived assuming that tides were semi-diurnal and that tidal inflow was equal to outflow each day. Linear interpolation between monthly samples was used to obtain daily values for stream inflow sediment and nutrient concentrations. Data from oceanographic research cruises in Foveaux Strait were used to derive tidal inflow nutrient concentrations (Bradford et al., 1991; Vincent et al., 1991). Chlorophyll *a* concentrations in inshore waters off the Southland coast tend to show a weak annual cycle, ranging from c. 0.2 μg L^{-1} in winter to 2–3 μg L^{-1} in late summer (Bradford et al., 1991; Murphy et al., 2001; Vincent et al., 1991), and these variations were assigned to the diatom group in the tidal inflow.

2.4. Model calibration and validation

DYRESM-CAEDYM was calibrated against field data (monthly surface samples collected at the lagoon sampling station) over the six-year period between October 2001 and October 2007 for variables of temperature, salinity, dissolved oxygen, chlorophyll *a*, dissolved reactive phosphorus, total phosphorus, ammonium, nitrate, total nitrogen, and total suspended solids at the water surface. The three simulated phytoplankton groups (i.e., cyanophytes, cryptophytes and diatoms) collectively contributed to a total simulated chlorophyll *a* concentration, which was calibrated against measured surface chlorophyll *a* (modelled phytoplankton chlorophyll *a* concentrations were also converted to g C m^{-2} to align units for comparative purposes with macrophyte and macroalgae biomass). Model parameters were adjusted manually using a trial and error approach, with values set to within literature ranges (e.g. Schladow and Hamilton, 1997; Özkundakci et al., 2011; Trolle et al., 2011). The model error was represented by a series of model performance statistics, including the root mean square error (RMSE), Pearson correlation coefficient (R), mean absolute error (MAE), and mean signed difference (MSD). Calibration continued until there was negligible improvement in model statistics with repeated model simulations. These model statistical metrics were also compared to those from modelling studies in the literature, to assess an acceptable model error for prediction purposes. The final calibrated model parameters were then fixed for model validation over the four-year period from November 2007 to October 2011 (Appendix B; Fig. B1 and B2).

There were limited data available on submerged macrophytes and macroalgae for calibration and validation of model output. Macrophyte surveys were carried out in March 2007, February 2009, February 2010 and March 2011. The survey methodology is described in detail in Robertson and Funnell (2012). Briefly, aerial photography and ground surveys were used to map submerged macrophyte beds and estimate percentage cover in 2007, and this was followed by benthic grab sampling at 48 sites in the lagoon in 2009, 2010 and 2011. Quantitative data on macrophyte percentage cover was gathered in all surveys, but there was no consistent quantitative data on macroalgae. Survey results indicate that macrophyte coverage in the lagoon declined from 2007 to 2011; macroalgae coverage increased from 2007 to 2010, and then declined in 2011 (Robertson and Stevens, 2009; Stevens and Robertson, 2007, 2010; Sutherland and Taumoepeau, 2011). An overall macrophyte percentage cover for the lagoon was estimated based on the survey data, with the caveat that the survey methodology is likely better suited to studying patch dynamics than assessing overall average percentage cover (Sutherland and Taumoepeau, 2011). Macrophyte biomass has not been measured in Waituna Lagoon, and only tentative relationships exist between percentage cover and biomass. For example, in Wilson Inlet, in the south of Western Australia, *R. megacarpa* biomass ranged from c. 5–70 g C m^{-2}, and percentage cover from c. 20–90% (Carruthers et al., 1999). In a model of the same system the maximum *Ruppia* biomass was assumed to be c. 180 g C m^{-2} (Haese and Pronk, 2011). In the absence of any Waituna-specific data, percentage cover was converted to biomass (in g C m^{-2}), based on a linear relationship with 100% cover equal to 100 g C m^{-2} (and 0% cover equal to 0 g C m^{-2}). Model error in simulating submerged macrophytes and macroalgae was not assessed statistically due to the small number of field data points and uncertainty around their derivation; rather the simulated variables were visually compared with the field data and the trends identified from the macrophyte surveys. Model sensitivity analyses were carried out on key parameters, boundary conditions and conceptual complexity (i.e., selected components of the conceptual model), and are described in Appendix D.

2.5. Scenarios

Scenarios were carefully chosen in order to better understand the range and direction of responses of Waituna Lagoon to different possible environmental and management regimes. The scenarios were not intended to provide definitive quantitative values for variables because it is not possible *a priori* to know, for example, the timing of lagoon closures, climate and its interaction with defined lagoon opening triggers. Instead the scenarios were designed to contribute to a body of knowledge to allow for informed environmental decision making. We designed 12 scenarios (including the baseline scenario) that varied the nutrient loading to the lagoon, lagoon openings, and climate (Table 1).

The nutrient loading scenarios represent “high” (i.e., 2001–2011, or actual/baseline) nutrient loading, “medium” (i.e., 50% of baseline loading) and “low” (i.e., 90% reduction of baseline loading). The baseline case had typically annual artificial openings of duration 34–330 days (Fig. 2). A scenario was constructed that was conceptualised as approximating a more natural opening regime, in which the barrier is not artificially opened and water breaches the lagoon for water exceed the lowest crest elevation of the barrier. In this scenario, water losses occur naturally through barrier seepage and evaporation. Barrier seepage was proportional to water levels and evaporation was accounted for within the DYRESM computation. Based on 2001–2011 input data, losses from barrier seepage and evaporation maintained water levels lower than the barrier, so the lagoon never “opened” in this scenario. Both the “no openings” and “artificial openings” scenarios were simulated across the range of nutrient loadings (i.e. “high”, “medium” and “low”).

Climate change scenarios were implemented in the model based on seasonal climate change projections provided for the Southland region of New Zealand (Ministry for the Environment, 2008). These projections indicate that by 2090 air temperature may increase by between 1.6 °C (in spring) and 2.1 °C (in winter), and rainfall may increase in spring and winter by 13 and 18%, respectively, based on mid-range estimates of projected changes relative to 1990. To simulate a future climate the seasonal increases in air temperature and rainfall were added to the baseline scenario. We assumed that increases in freshwater inflows would be in proportion to increases in rainfall, which was considered appropriate in the absence of a catchment hydrological model. This “future” climate scenario was simulated for both the “no openings” and “artificial openings” scenarios, and across the range of nutrient loading scenarios, to explore potential interactive effects of climate change and

Table 1
Summary of scenarios that were simulated with the DYRESM-CAEDYM model of Waituna Lagoon.

Lagoon opening regime	Climate	High nutrient load	Medium nutrient load	Low nutrient load
Artificial openings	Current climate	Scenario #1	Scenario #2	Scenario #3
Artificial openings	Future climate	Scenario #4	Scenario #5	Scenario #6
No opening	Current climate	Scenario #7	Scenario #8	Scenario #9
No opening	Future climate	Scenario #10	Scenario#11	Scenario #12

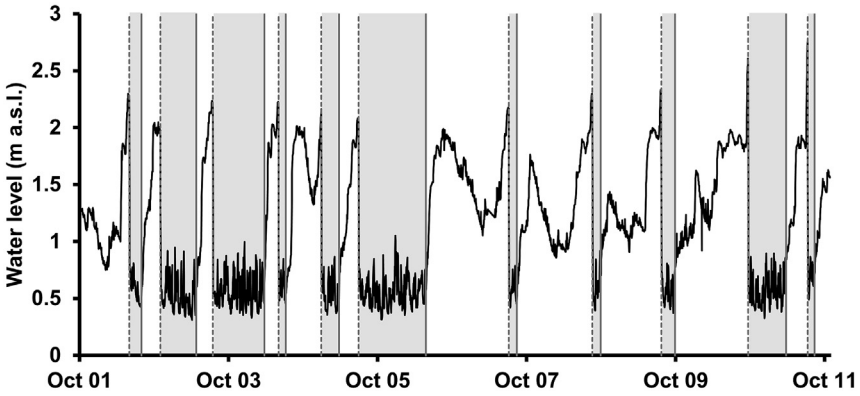

Fig. 2. Waituna Lagoon water level (black line), with periods during which lagoon was open indicated with grey shading.

management options on ecosystem dynamics.

3. Results

3.1. Model calibration and validation

Visual representations of modelled output against all available field measurements are presented in Appendix B. Model performance statistics (Table 2) suggest that the model reproduced the magnitude and dynamics of field measurements using parameters values consistent with published values (Appendix C), and performed well compared to other published model applications for lakes (e.g., Burger et al., 2008; Gal et al., 2009; Fragoso et al., 2011; Özkundakci et al., 2011; Trolle et al., 2011). The model reproduced chlorophyll *a* variations associated with periods of low (<3 μg L^{-1}) phytoplankton biomass, but did not perform as well for periods of high (>12 μg L^{-1}) chlorophyll *a* concentrations. Error statistics for the calibration period suggest the model was most successful at simulating nitrate, total nitrogen, temperature, and salinity. Where model statistics suggested that the model performed less well, e.g., for dissolved reactive phosphorus and ammonium, a high proportion of the observations (between 25 and 40%) were below analytical detection limits, which can restrict the ability of statistics to define model error; this is particularly true for the Pearson correlation coefficient. Error statistics for the validation period indicated that the model performance is comparable to that for the calibration period.

Visual comparison of modelled macrophyte biomass with available field survey data shows that the model generally reproduced the declining trend identified in field surveys from 2007 to 2011. While macroalgae biomass was not quantified during field observations, reports from macrophyte surveys suggested that macroalgae abundance increased from 2007 until 2010, but then decreased in the summer of 2011, a pattern that was also represented by the model (Appendix B, Fig. B2).

3.2. Effect of scenarios on primary producer groups

3.2.1. Baseline scenario (2001–2011)

Under the baseline scenario (Scenario #1) there were pronounced fluctuations in macrophyte and macroalgae biomass (Fig. 3). For the first half of the simulation period (2001–2006) the biomass of all three primary producer groups was low, but from 2006 to 2011 macrophyte biomass initially increased and then

Table 2
Statistical comparison of DYRESM-CAEDYM model simulations with field data (monthly measurements) of surface water in Waituna Lagoon, using Pearson correlation coefficient (R), root mean square error (RMSE), mean absolute error (MAE), and mean signed difference (MSD) for each variable.

Variable	Calibration (July 2001–June 2007)				Validation (July 2007–June 2011)			
	R	RMSE	MAE	MSD	R	RMSE	MAE	MSD
Temperature (°C)	0.94	1.57	1.24	0.06	0.97	2.66	1.43	0.54
Salinity (psu)	0.97	3.10	1.99	−0.97	0.96	3.37	2.07	−0.69
Dissolved oxygen (mg L^{-1})	0.46	1.27	1.00	0.25	0.43	1.60	0.82	−0.47
Dissolved reactive phosphorus (mg L^{-1})	0.16	0.015	0.009	−0.005	0.67	0.011	0.006	0.005
Total phosphorus (mg L^{-1})	0.14	0.031	0.020	−0.006	0.34	0.031	0.021	0.004
Nitrate-N (mg L^{-1})	0.89	0.206	0.161	0.090	0.92	0.254	0.185	−0.005
Ammonium-N (mg L^{-1})	0.57	0.016	0.013	0.004	0.77	0.021	0.017	0.011
Total nitrogen (mg L^{-1})	0.77	0.364	0.284	0.001	0.89	0.427	0.314	−0.162
Chlorophyll *a* (μg L^{-1})	0.39	6.18	3.82	−1.99	0.30	6.20	3.38	−1.01
Total suspended solids (mg L^{-1})	0.30	5.40	3.93	−1.03	0.11	6.05	4.25	−0.32

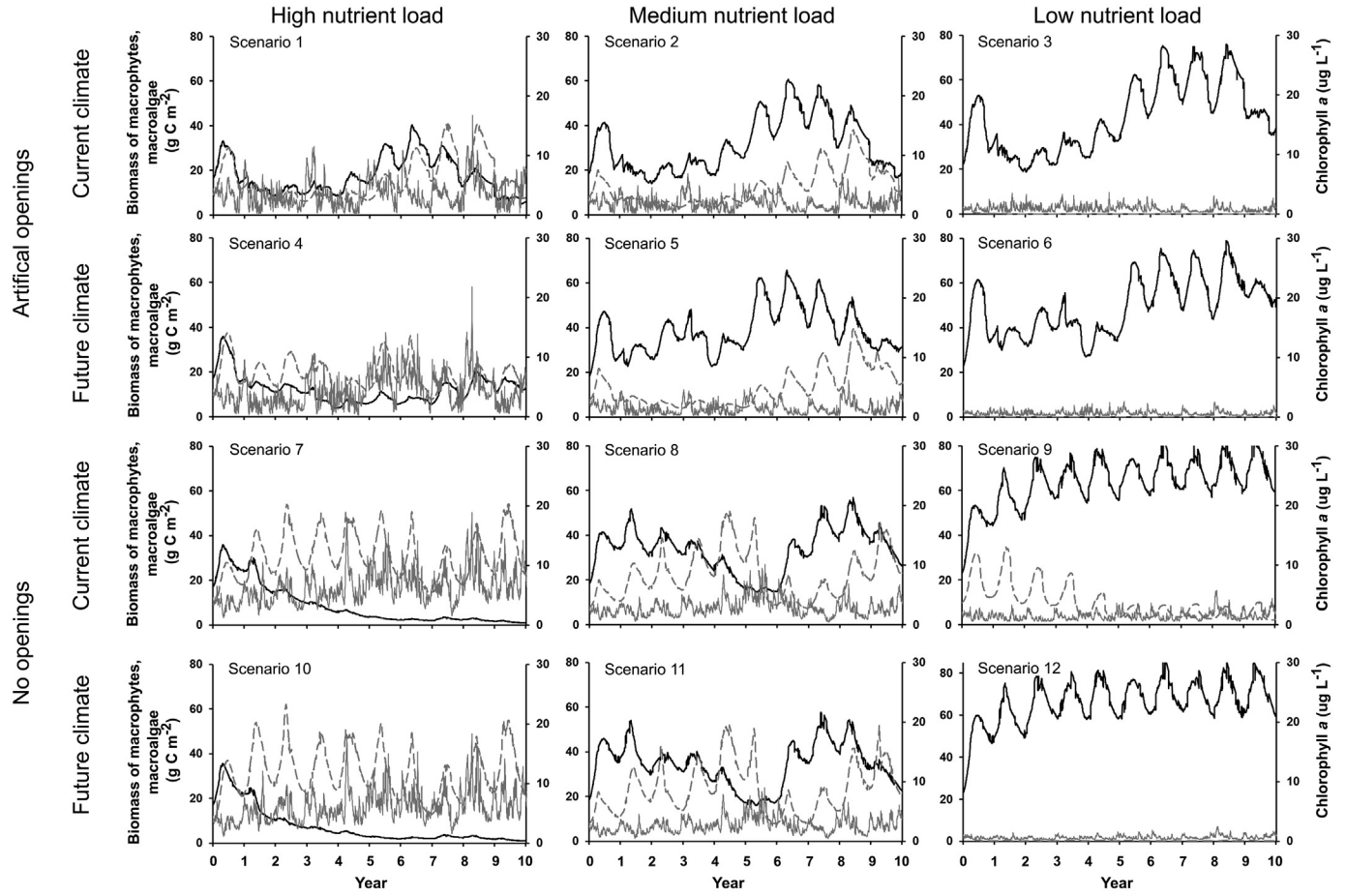

Fig. 3. Macrophyte biomass (black line; primary vertical axis), macroalgae biomass (grey dotted line; also primary vertical axis), and chlorophyll *a* concentration (grey solid line; secondary vertical axis) under nutrient loading, opening, and climate change scenarios (scenarios are numbered according to Table 1). Simulations ran for ten years; the top left panel (high nutrient load, artificial openings, current climate) is the baseline scenario (i.e. 2001–2011). Note: Macroalgae simulation output may not be visible in all panels due to low biomass.

declined rapidly as macroalgae biomass and chlorophyll *a* concentrations increased. A rapid decline in macroalgae and chlorophyll *a* was evident near the end of the simulation.

3.2.2. Effects of other scenarios

Nutrient load reduction scenarios (Scenarios #2 and #3) resulted in increased macrophyte biomass, and decreased macroalgae biomass and chlorophyll *a* concentration (Fig. 3). Chlorophyll *a* concentrations generally decreased proportionally to the changes in nutrient loading to the lagoon. For example, average chlorophyll *a* concentration decreased from 3.6 μg L^{-1} under the high nutrient load scenario (Scenario #1) to 1.9 μg L^{-1} under the medium nutrient load scenario (50% reduction compared to baseline; Scenario #2). Average macrophyte biomass increased by c. 80% and 250% with a nutrient load reduction of 50% and 90%, respectively.

Scenarios with no lagoon openings led to higher and less variable water levels compared to scenarios with artificial openings. Under high nutrient loads and no openings (Scenarios #7 and #10), both chlorophyll *a* concentration and macroalgae biomass increased, and macrophyte biomass decreased to concentrations < 2 g C m^{-2}, which ultimately resulted in permanent loss of the macrophyte population during the simulation period. Under medium nutrient loads and no openings (Scenarios #8 and #11), chlorophyll *a* concentration remained comparably high during the simulation period (up to 10 μg L^{-1}), whereas under low nutrient loads and no openings (Scenarios #9 and #12) macrophyte biomass increased substantially over the entire simulation (up to 84 g C m^{-2}) and macroalgae and chlorophyll *a* declined to low levels (c. 3 g C m^{-2} and 2 μg L^{-1}, respectively).

Under future climate scenarios, water levels were typically higher in winter (due to increased rainfall and runoff) and lower in summer (due to increased evaporation associated with higher temperatures) compared to scenarios for current climate. Under high nutrient loads, the future climate scenario (Scenario 10) led to an increase in macroalgae biomass and chlorophyll *a* concentrations (overall increase of 18% for both) and decrease in macrophyte biomass (30% on average over the simulation period), compared to the current climate (Fig. 3). The opposite effect was apparent under low nutrient loads, with an increase in macrophyte biomass and decrease in macroalgae and chlorophyll *a* under the future climate scenario, compared to the current climate, with both no openings and artificial openings (Scenarios 9 and 12).

The modelled total biomass of primary producers responded strongly to both the nutrient load reduction and lagoon opening regime scenarios, with the climate change scenario having a more subtle effect (Fig. 4). Apparent interactive effects of multiple disturbances were evident based on scenarios that combined nutrient load reductions with changes in climate or opening regime. For example, climate change increased total biomass of primary producers compared with the baseline scenario (e.g., from 210 g C m^{-2} in Scenario 1–240 g C m^{-2} in Scenario 4). This effect was less pronounced in combination with nutrient load reductions, but the

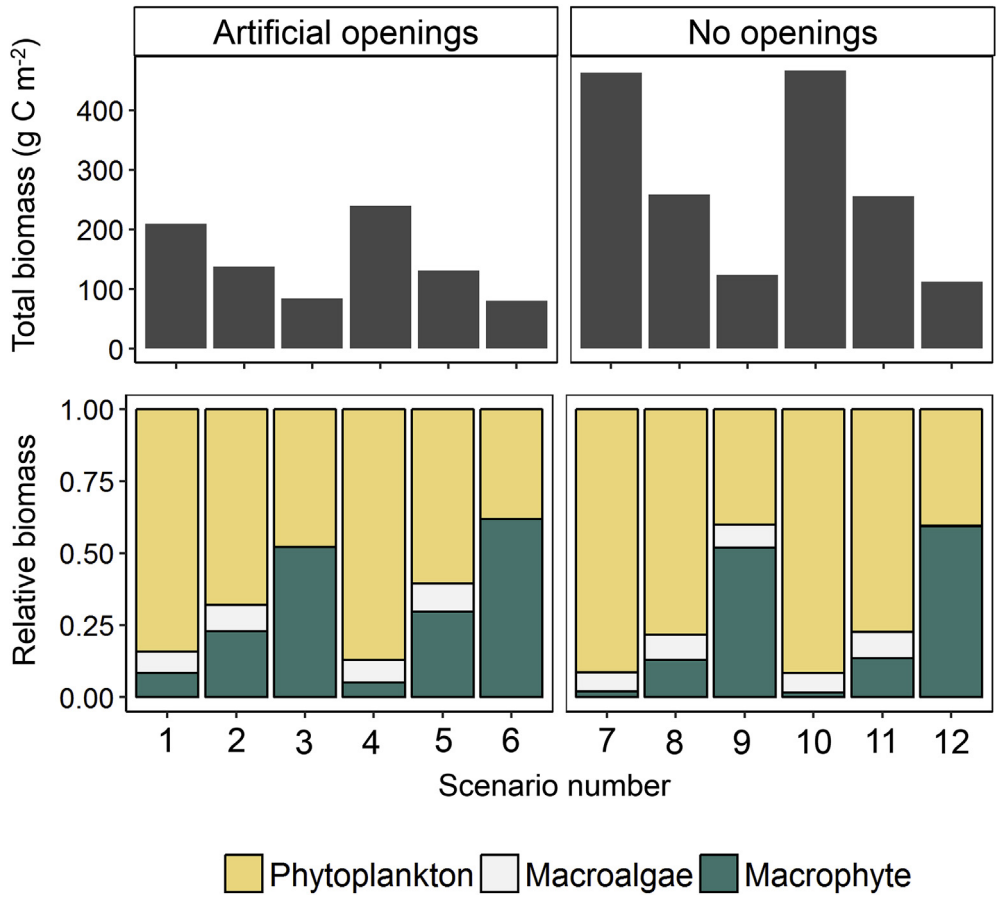

Fig. 4. Total biomass of simulated primary producers (top panels) and relative biomass of simulated primary producers (bottom panels) averaged over the entire simulation period (i.e. 10 years). Scenarios are separated into those that include artificial openings and no openings. Scenarios are numbered according to Table 1.

relative biomass contribution of primary producer groups was altered. The effect of not opening the lagoon to the sea resulted in a 2.2-fold increase in average total biomass (from 210 g C m^{-2} in Scenario 1–462 g C m^{-2} in Scenario 7) and greater dominance of phytoplankton (84% of total primary producer biomass versus 91%, respectively). With nutrient loads severely reduced the effect on primary producer biomass of not opening the lagoon was less pronounced, however the effect of not opening the lagoon to the sea resulted in only a 1.2-fold increase in average total biomass at "low" nutrient loads.

4. Discussion

4.1. Effects of multiple disturbances on the coastal lake ecosystem

By applying a complex dynamic process-based ecological model to Waituna Lagoon, New Zealand, we have identified interactive effects of multiple stressors on primary producer biomass in this coastal lake. These stressors can interact either antagonistically (e.g., in the case of artificial openings, and high nutrient loadings), or synergistically (e.g., in the case of high nutrient loading and climate change).

Artificial opening regimes of this type can be used to mitigate eutrophication of coastal lakes (i.e., to flush nutrients from the system), and appear to be crucial for sustaining a submerged macrophyte population in this particular case (Schallenberg et al., 2010). The importance of barrier openings for flushing excess nutrients and phytoplankton from the lagoon has been identified in previous studies (e.g., Schallenberg et al., 2010, 2017) and is evident from both modelled and measured nutrient concentrations, which show a dramatic decrease following opening events. Primary producer dynamics in our baseline scenario appear to be linked to lagoon openings. Lagoon openings were typically long (c. 100–300 days) during the period 2001–2006 when biomass of all three primary producer groups was low. From 2006 to 2011, lagoon openings were typically short (c. 40–70 days), and macrophyte biomass initially increased and then declined rapidly as macroalgae biomass and chlorophyll *a* concentration both increased. No lagoon openings may negate reductions in external nutrient loading and may increase phytoplankton dominance unless substantial reductions in nutrient loading (90% in our simulations) are achieved. The ecological effects of climate change partially negate decreases in nutrient loading and exacerbate the effect of no lagoon openings when nutrient loads remain high. Macrophyte dominance (as assessed by biomass) was only achieved in the most extreme scenarios in our study (i.e., 90% reduction in external nutrient loads).

With no artificial lake openings, the absence of regular tidal flushing of nutrients promoted growth of phytoplankton and macroalgae. Based on our model, a mechanistic explanation may be that due to increased shading by macroalgae, submerged macrophyte biomass decreased, enhancing resuspension of sediments and phytoplankton, and thus increasing light limitation of submerged macrophytes. Subsequently, high phytoplankton biomass shaded macroalgae, and macroalgae biomass then decreased. This is consistent with research showing that increasing eutrophication in coastal systems results, firstly, in the replacement of submerged

macrophytes (e.g., seagrasses) with macroalgae, and secondly, the replacement of macroalgae by phytoplankton (Valiela et al., 1997; Teichberg et al., 2010). This may be exacerbated by physical detachment of macroalgae under high shear stresses as cells near the base of the bed receive insufficient light for photosynthesis to compensate respiratory losses (Higgins et al., 2008). Shading by epiphytic algae has also been identified as a cause of seagrass loss in many Australian estuaries (Walker and McComb, 1992). Modelling results and field observations indicate that, under current nutrient loads, the flushing and frequent disturbance caused by lagoon openings have, to date, prevented a long-term shift to an algae-dominated state.

Managing lagoon openings to sustain an abundant submerged macrophyte population in Waituna Lagoon has previously been described as a "trade off" because openings were perceived to exert both positive (reducing the effects of eutrophication) and negative impacts (desiccation and salinity stress) on submerged macrophytes (Robertson and Funnell, 2012). However, the dominant submerged macrophytes in Waituna Lagoon are typically *Ruppia polycarpa* and *R. megacarpa* which are well adapted to live in environments with fluctuating water levels and salinity (Brock, 1982). *R. megacarpa* is a perennial plant and is typically found in permanently saline waters and *R. polycarpa* is an annual that reproduces using both seeds and turions (asexual propagules) and is often found in seasonally inundated saline lakes and ponds (e.g. Snoeijs and van der Ster, 1983; Carruthers et al., 2007). However, the extent to which frequent desiccation of macrophyte beds (e.g., from regular openings) may affect the resilience of the system by, for example, depleting seed banks (which are not represented by the current model) appears to be largely unknown and may represent another source of disturbance acting over a longer time scale.

Regime shift theory of shallow lakes (*sensu* Scheffer et al., 1993) predicts that at low nutrient loads, primary producers in aquatic ecosystems should be dominated by submerged macrophytes. Furthermore, it is suggested that across a range of moderate nutrient loads, the system may be dominated either by macrophytes or phytoplankton, with shifts between the two initiated by stochastic disturbances, such as storms or water level variation. While we did not explicitly develop simulation scenarios to test these predictions, our results show that at intermediate nutrient loads, macrophyte or phytoplankton biomass in Waituna Lagoon is indeed highly variable, and appears to be related to water levels in the lagoon (which influence available habitat for submerged macrophytes, as well as nutrient concentrations and algal productivity). By contrast, a major storm event completely destroyed submerged macrophyte beds in Te Waihora (Lake Ellesmere), and since then very high suspended sediment and chlorophyll *a* concentrations have prevented any substantial regeneration of submerged macrophytes (Gerbeaux and Ward, 1991; Schallenberg et al., 2010). Lake Ellesmere is much larger than Waituna Lagoon (surface area 160–200 km^2 cf. 10–20 km^2), and the increased fetch likely results in very high rates of resuspension, apparently inhibiting macrophyte re-growth. In contrast, results from this study suggest that submerged macrophytes have been able to persist in Waituna Lagoon, despite high nutrient loads, although this may not be the case under scenarios with no openings, which lead to higher water levels and increased algal biomass (see Figs. 3 and 4). Water level fluctuation has previously been identified as a likely cause of regime shifts; for example, high water levels during the growing season reduce light availability for submerged macrophytes and may initiate a regime shift towards phytoplankton dominance (e.g. Randsalu-Wendrup et al., 2016). Salinity may also interact with variations in water levels to control submerged macrophyte dominance, as noted in the East Kleinemonde estuary in South Africa (e.g. Riddin and Adams, 2012).

The simulated climate change scenarios further suggest that future management of the lagoon should begin to factor in more stringent nutrient load controls. Under high (current) nutrient loads, a warmer and wetter climate resulted in decreased submerged macrophyte biomass, and increased phytoplankton biomass (Fig. 3). The effect was most obvious under the artificial openings and future climate scenario, where the macrophyte biomass decreased to low levels (<20 g C m^{-2}) throughout the simulation period. This is consistent with research that suggests the effects of a warming climate on shallow lake and lagoon ecosystems will be to stabilise turbid, phytoplankton-dominated states and/or destabilise clear water, macrophyte-dominated states (Lloret et al., 2008; Mooij et al., 2005). Changes in wind speed due to climate change are still highly uncertain, and were not considered for climate change scenarios in this study. However, projections for Southland indicate increases in wind speed (Ministry for the Environment, 2008), which would likely further stabilise a turbid state by increasing rates of bed resuspension and reducing opportunities for macrophyte re-establishment. Conversely, under low nutrient loads and "future climate" scenarios, macrophyte biomass increased and phytoplankton biomass decreased. This result reinforces predictions that aquatic ecosystems may be more resilient to climate change, particularly to eutrophication, if other stressors such as eutrophication are reduced (e.g. Brookes and Carey, 2011; Folke et al., 2004).

The results of this study suggest that in coastal lakes, chronic disturbance from both eutrophication and climate change may induce shifts to phytoplankton-dominated states, but that artificial disturbance in the form of artificial openings may prevent or reverse such regime shifts. When placed in the context of regime shift theory for shallow lakes (*sensu* Scheffer) these results indicate that the range of nutrients loads over which both submerged macrophyte and phytoplankton dominance is possible may be extended for coastal lakes due to the potential for frequent disturbance from opening events. That the climate change scenario induced a shift to long-term phytoplankton dominance under current nutrient loads and openings regimes may provide impetus to review the current management of this coastal lake and similar systems, particularly as many lowland lakes and coastal systems are under intense pressure from rapid land use intensification in New Zealand (Drake et al., 2010). Our modelling shows that reducing nutrient loads is imperative to sustaining submerged macrophyte populations, given the impacts of likely future climate change, and/or if the frequency of artificial openings were reduced. The model has used as part of a body of evidence to reach a consensus amongst scientists, stakeholders, managers and iwi, on the nutrient load reductions required to sustain the macrophyte population in Waituna Lagoon (Schallenberg et al., 2017).

4.2. Model performance

The performance of the calibrated model was generally satisfactory, typically simulating the timing and magnitude of all modelled variables. Where the model did not perform well, field measurements were often close to or below analytical detection limits, making for considerable uncertainty in the field data against which the model performance was assessed statistically. Although the model captured the timing and magnitude of elevated phytoplankton biomass and periods of low phytoplankton biomass, it did not capture some of the high-chlorophyll *a* field measurements. It is likely that some of these events may have been highly localised, and hence not represented in the one-dimensional (horizontally-averaged) model, and/or possibly driven by extreme (and short-lived) resuspension events. Meteorological input data were obtained from a climate station some distance (c. 15 km) from the

lagoon, and thus may have affected the ability of the model to capture wind-driven resuspension events accurately. Furthermore, as model input typically consisted of interpolated monthly samples for freshwater inflows, it may not have been able to reproduce short-lived increases in phytoplankton biomass resulting from periods of elevated nutrient loading not captured by monthly monitoring. This highlights the importance of accurate and high-resolution forcing data for predicting short-term (i.e. days to weeks) variability in phytoplankton biomass (e.g., Kara et al., 2012).

There were limited field data available for calibrating and validating submerged macrophytes and macroalgae, and conversion of field survey data (measured as percent cover) for submerged macrophytes to biomass is confounded by the lack of any direct biomass measurements in the lagoon. Furthermore, the sensitivity analysis indicates that the model formulation for submerged macrophytes and microalgae growth is sensitive to changes in growth parameters (see Appendix D). However, the model reproduced the trajectory identified in field surveys for submerged macrophytes and macroalgae, and simulation of other variables (particularly chlorophyll *a* and dissolved reactive phosphorus) improved considerably after including these two groups as well as a dynamic feedback between submerged macrophyte biomass and resuspension. The calibrated model imposed only a modest salinity limitation on growth of submerged macrophytes (see parameter values in Appendix C), because a review of available literature indicated that although *R. polycarpa* may sometimes respond positively to fresh/brackish water, *Ruppia* spp. are typically adapted to live in environments with fluctuating salinity (e.g. Carruthers et al., 2007; Sim et al., 2006; Smith et al., 2009).

4.3. Model limitations

Conceptual simplifications of a modelled system are unavoidable (e.g. Harris, 1994), and we recognise that omission of species and processes that may affect model output. However, it is important to note here that increasing model complexity increases the number of model parameters required and thus contributes to greater complexity and uncertainty in model output; as well as increasing the amount of data required to be collected for model validation (e.g. Loucks et al., 2005). In this study, zooplankton and fish were omitted due to a lack of field data with which to parameterise, calibrate and validate the model. Moreover, dynamics of zooplankton and fish assemblages in Waituna Lagoon are dependent on whether the lagoon is open or closed, and there is no clear indication of persistent dominance by larger grazers (e.g., *Daphnia* sp.) that are likely to exert direct control on phytoplankton biomass (Schallenberg et al., 2003; Duggan and White, 2010).

Many submerged macrophytes are rooted in bottom sediments, where nutrient availability is typically much greater than in the water column; porewater nutrient concentrations may be orders of magnitude higher than in overlying water (e.g. Wu et al., 2001; Lohrer et al., 2010). It was assumed that all submerged macrophyte nutrient uptake was from the bottom sediments and therefore water column nutrients did not limit growth. However, some submerged macrophyte species may take up nutrients from the water column (e.g., see Dudley et al., 2001), so the assumption of sediment nutrient uptake may have implications for determining the role of submerged macrophytes as a nutrient sink in the lagoon. There does not appear to be a consensus in the literature on the relative importance of water column or sediment nutrient uptake (which is also the case for species found in Waituna Lagoon), and considerable variation in nutrient uptake and metabolism has been shown by both seagrass (Burkholder et al., 2007) and freshwater macrophyte species (Mi et al., 2007). Nitrate toxicity on submerged macrophytes was not included in the model, as toxicity effects on submerged macrophytes are not consistent amongst studied systems and may be species-specific, or dependent on other factors such as temperature (Burkholder et al., 1994; Nelson, 2009; van Katwijk et al., 1997). Further model development would require controlled experimental studies to enable development and parameterisation of the processes specific to macrophyte nutrient uptake rates and the possible effects of nitrate toxicity on macrophyte species in coastal lakes.

Sediment nutrient dynamics implemented in CAEDYM for this study comprise a relatively simplistic process representation, with sediment nutrient release regulated by water column variables only, i.e., not by sediment nutrient content, as discussed in other DYRESM-CAEDYM applications (e.g. Özkundakci et al., 2011; Trolle et al., 2011). Internal loading from releases of dissolved nutrients may be relatively small compared to external loading from catchment inflows (which are substantial, see Appendix A; Table A1). Changes in the sediment redox environment, for example, a transition to reduced oxygen status due to further increases in external nutrient loading, may induce higher rates of release of dissolved nutrients (e.g., Penn et al., 2000). Thus, the current model configuration may not be suitable for simulating scenarios involving long-term feedbacks between changes in catchment nutrient loads and responses of bottom-sediment nutrient releases (none were included in the present study). The inclusion of such feedbacks into a dynamic model may ultimately allow the formulation of scenarios that explicitly test the equilibrium behaviour of the Waituna Lagoon ecosystem in a regime shift framework (Scheffer et al., 1993). Accounting for model sensitivity to parameter changes (Appendix D) would be of upmost importance and could be addressed by carefully designing experiments and monitoring campaigns. Surveys of bottom- nutrient composition and physico-chemical status (e.g., redox profiles) of bottom sediments could usefully be integrated into future monitoring to identify responses of bottom sediments to altered nutrient loads and provide validation for development of more sophisticated sediment modules.

5. Conclusions

Using a complex process-based ecological model for a coastal lake we have explored scenarios that incorporate multiple disturbances which may initiate, or provide resilience to, shifts in biomass dominance of primary producers. The model provides a tool which can be applied to the management of a coastal lake influenced by catchment development and artificial openings. Our results indicate that in this coastal lake exposed to high rates of external nutrient loading, the frequent disturbances caused by artificial openings prevent a long-term persistent regime shift to an algae-dominated state. However, under current nutrient loading, climate change is likely to enhance the effects of eutrophication on the system. Were external nutrient loading to be substantially reduced, the scenarios indicate that restoration of submerged macrophyte populations may be possible under a management regime that does not involve artificial openings.

Our modelling shows that chronic disturbances (i.e., increases in anthropogenic nutrient loading and climate change) and rapid disturbances (i.e., artificial openings) can potentially work interactively to prevent or initiate regime shifts. The response of a coastal lake ecosystem to chronic eutrophication can thus be significantly affected by artificial or natural disturbance, and the potential for such disturbances must be carefully considered for effective management of these ecosystems. These patterns are likely to be applicable to other coastal lakes. Ecological modelling increasingly plays an important role in decision-making for the management of aquatic ecosystems; models such as the one developed for this study provide site-specific information on

trajectories of change under different scenarios, and contribute to the growing body of knowledge on the response of these ecosystems to natural and anthropogenic stressors.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jenvman.2017.11.063.

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